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the hills of ancient Rome in the number and variety of Vultures that I have been able to discern.

With Dr. Allen's closing statement that the first species rule 'has only here and there a disciple' or that it has ever been generally abandoned *in practise* so far as ornithology is concerned, I beg to differ.

The interviews and correspondence that I have had since my paper was published show that the adoption of the first species rule as there outlined meets with very general approval among vertebrate zoologists as well as entomologists, while botanists, as is well known, have long practised it.

One prominent entomologist in a recent publication hopes that it may be incorporated in the International Code at an early date, while one of the foremost zoologists of America writes me that "elimination is absolutely dead and ought not to be revived in any code or thought of in any connection."

A thorough discussion of this subject is desirable, but really, my friend Dr. Allen and I are of nearly the same mind on the question. He says at the beginning of his article: "I have always conceded that this [*i. e.*, the first species principle] would be the ideal method if we were at the threshold of our work \* \* \* and my opposition to it has been \* \* \* that to adopt it now would introduce serious confusion into nomenclature." This was exactly my view, and when upon investigation I found that serious confusion (so far as birds are concerned) would not ensue, I thought that there were no further grounds for objection. The other objections that have occurred to Dr. Allen in the later pages of his paper I have tried to dispel.

At the present time I feel more sure than ever that the zoological code that adopts the first species rule (excepting in relation to Linnaeus) will be setting an example which will in a few years be followed by vertebrate zoologists in general and, with a possible **further** limitation, by invertebrate zoologists as well.

WITMER STONE

ACADEMY OF NATURAL SCIENCES  
OF PHILADELPHIA

# SPECIAL ARTICLES

## ON A CASE OF REVERSION INDUCED BY CROSS-BREEDING AND ITS FIXATION<sup>1</sup>

PERHAPS the most important extension which has been made of the law of heredity originally discovered by Gregor Mendel consists in the demonstration (chiefly by Cuènot and Bateson) that certain characters are produced only when two or more separately heritable *factors* are present together. Such a character does not conform with the simple Mendelian laws of inheritance, but its *factors* do. Herein lies the key to the explanation of so-called *heterozygous* characters and to the practical process of their fixation. This same principle serves to explain also atavism or *reversion*, and the process by which reversionary characters may be fixed.

When pure-bred black guinea-pigs are mated with red ones, only black offspring are, as a rule, obtained. The hairs of the offspring do indeed contain some red pigment, but the black pigment is so much darker that it largely obscures the red. In other words, black behaves as an ordinary Mendelian dominant. In the next generation black and red segregate in ordinary Mendelian fashion, and the young produced are in the usual proportions, three black to one red. All black races behave alike in crosses with the same red individual, but among the reds individual differences exist. Some, instead of behaving like Mendelian recessives, produce in crosses with a black race a third apparently new condition, but in reality a very old one, the agouti type of coat found in all wild guinea-pigs, as well as in wild rats, mice, squirrels and other rodents. In this type of coat red pigment alone is found in a conspicuous band near the tip of each hair, while the rest of the hair bears black pigment. The result is a brownish or grayish ticked or grizzled coat, doubtless inconspicuous and so protective in many natural situations. Some red individuals produce the reversion in half of their young by black mates, some in all, and others, as we have seen, in none, this last condition being the commonest of the three. It is evident that the

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reversion is due to the introduction of a third factor, additional to simple red and simple black. It is evident further that this new third factor, which we will call *A* (agouti), has been introduced through the red parent, and that as regards this factor, *A*, some individuals are homozygous (*AA*) in character, others are heterozygous (transmit it in half their gametes only), while others lack it altogether. Further observations show that it is *independent* in its inheritance of both black and red; it is, in fact, an independent Mendelian character, which can *become visible* only in the presence of both black and red, because it is a mosaic of those two pigments.

The reversionary individuals (agoutis) do not breed true. They produce offspring of three sorts, agouti, black and red. When mated *inter se*, they produce young in the proportions, 9 agouti: 3 black: 4 red; when mated with reds (recessives), they produce young in the proportions 1 agouti: 1 black: 2 red.

It has been found by experiment that the  $F_2$  agoutis (produced by mating the original agoutis *inter se*) are of three different sorts. It is probable that they are in reality of four different sorts. The three sorts thus far recognized are (1) agoutis like their parents, which produced the three sorts of young, agouti, black, and red in the proportions already stated; (2) agoutis which in matings with recessives (reds) produced only agouti young and red young in equal proportions; (3) agoutis which in matings with red animals produced *no red offspring*, but only agouti ones and black ones in equal numbers. The fourth (expected) class should when mated with reds (or any other color, for that matter) produce only agouti colored young; *i. e.*, should not only *resemble* wild guinea-pigs in the character of its coat, but should transmit this character to all its young, as wild ones do. This is on the hypothesis already stated that the factor *A* is a distinct Mendelian character. The gametic constitution of the four classes of agoutis would on this hypothesis be:

1.  $RA \cdot B$ , forming gametes *R*, *RA*, *B*, and *BA* with equal frequency.

2.  $RA \cdot BA$ , forming gametes *RA* and *BA* with equal frequency.

3.  $BA \cdot B$ , forming gametes *BA* and *B* with equal frequency; all these classes have been proved to exist.

4. The fourth (expected) class, the fully fixed agouti, known to exist but not yet produced in this experiment, should have the formula  $BA \cdot BA$  like class 2 in that *A* is transmitted in all its gametes, but differing from it in that black also is transmitted in *all* the gametes, instead of in half of them only.

But, some one may inquire, how is it that an individual which forms *no* red gametes (as  $B \cdot BA$  or  $BA \cdot BA$ ) can nevertheless produce agouti young, which character is by hypothesis a mosaic of red with black. This is a matter which gave me considerable trouble and made the at first wholly unexpected class 3 ( $B \cdot BA$ ) for a long time perplexing. The explanation is this: Ordinary black individuals, while homozygous, are not pure in the sense that they form no pigment but black. They probably always form a certain amount of red and of brown pigment, which is overlooked only because it is interspersed with the more opaque black pigment. If the red pigment is segregated, as is the case when the factor *A* is present, then it becomes visible as the agouti marking of the hair. If this factor, *A*, is present in both halves of the zygote together with black (and enough red to form the agouti hair tip) a homozygous agouti animal is the result (class 4); if *B* is present in both halves of the zygote, but *A* in one half only, agouti and black young will be produced.

The existence of a third factor, *A*, in cases of reversion in coat-character among rodents has been heretofore overlooked merely because it does not represent a distinct pigment or set of pigments, but consists in a particular kind of pigment distribution on the individual hairs. The agouti hair is due to a definite cycle of activity of the hair follicle in forming its pigments, first black, then red, then black; the wholly black hair is due to a continuous process of pigment formation without alternation in the character of the pig-

ments produced. The relation between agouti and black is precisely the same as that between short hair and long hair due likewise to differences in follicle activity, as I have elsewhere shown, but inherited quite independently of hair pigmentation. Short hair is the result of a determinate growth cycle; the hair grows so long and then stops growing; long or angora hair is the result of indeterminate activity on the part of the hair follicle; the hair keeps growing so long as its follicle is alive.

We are now able to give a rational explanation of the *origin* of the various color varieties of rodents. The wild cavy transmits *in all its gametes* the three factors *A*, *B* and *R*. By accident (mutation) a gamete has been formed which lacked *A*. When two such gametes came together the result is a black individual, *and this individual will breed true*. Here is the explanation of our occasional black squirrels, porcupines and the like. If by a further mutation *B* is lost, leaving *R* alone, a red race is produced which will breed true and *will not give reversion on crossing with blacks*. Such are ordinary red guinea-pigs.

But if mutation is directly from the wild or agouti condition, *ABR*, by loss of *B*, leaving *AR*, then there is produced a red not different from ordinary reds in appearance, but which will give reversion in crosses with black.

The albino mutation, which is frequently found in wild as well as in tame rodents, is not due, as might be supposed, to simultaneous loss of the three factors *A*, *B* and *R*, for albinos can be shown to possess, some one, some two and some all three of these factors. They have, according to Cuènot, lost a certain other factor necessary for the production of pigment of any kind, an activating or ferment-like factor.

It has been observed that one mutation is often followed by another. De Vries in his *Mutationstheorie* speaks repeatedly of *periods of mutation*. We can begin to see the significance of this; given one mutation, we can produce others.

Suppose, for example, that we possess agouti and ordinary red varieties only and desire

black, we are not compelled to await a mutation to produce it; we can cross red with agouti and obtain black in the second generation. This is not hypothesis merely; its correctness has already been in part demonstrated. Thus, in one experiment, there was employed an agouti of the formula  $AB \cdot AR$ , which gave only reds and agoutis in crosses with red, but the agoutis so produced when mated in the same way as the parent gave blacks as well as reds and agoutis, for they were of the formula  $AB \cdot R$ . From such animals homozygous blacks ( $B \cdot B$ ) are readily obtained.

To produce a red variety from agoutis and blacks alone would not be so easy; it would be necessary either to await a mutation or to work by the slow process of selection from continuous variations in the intensity of blacks under cross-breeding with agoutis. In mice and rabbits as well as in guinea-pigs red (or yellow) varieties are well known, but in rats yellow has never been obtained separate from black, though black and agouti varieties are common, both wild and in captivity.

We now know what the 'fixation' of a heterozygous character implies. When *A* and *B* are crossed, we obtain *C*. *C* is due either simply to co-existence of *A* with *B*, or to the co-existence with them of a third factor introduced with one or the other. In either case fixation will consist in getting *into the gamete* all the factors which produce *C*. In the first case, the zygote is  $A \cdot B$ , and the resultant is equivalent to *C*. Fixation will consist in getting a zygote of the formula  $AB \cdot AB$ ; every gamete produced will then bear the equivalent of *C*, viz., *AB*. In the second case, the zygote is either  $AC \cdot B$  or  $A \cdot CB$ ; fixation will consist in obtaining a zygote,  $ACB \cdot ACB$ ; every gamete formed will then contain the three factors, *A*, *C* and *B*. W. E. CASTLE

ZOOLOGICAL LABORATORY,  
HARVARD UNIVERSITY,  
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#### BOTANICAL NOTES

##### THE RUSTS OF AUSTRALIA

UNDER this title D. McAlpine, the government pathologist of Victoria, Australia, prepared a book of 350 pages, which has been